

SOIL-OXYGEN EFFECTS ON STOMATAL RESPONSE

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ABSTRACT

We reviewed and compared several greenhouse studies on the effects of low soil oxygen (O_2) levels upon plant response. The studies are discussed with particular reference to stomatal closure. Both indirect and direct observations of stomatal closure at low soil O_2 diffusion rates (ODR) were compiled. Plant response was similar over a wide range of species, including tomato (*Lycopersicon esculentum*), sunflower (*Helianthus*, sp.), jojoba (*Simmondsia chinensis*), cotton (*Gossypium hirsutum* and *G. barbadense*), and wheat (*Triticum aestivum*). The studies reviewed indicate that elimination of soil O_2 from the profile can cause stomatal closure even at optimum matric potentials. When ODR dropped below $20 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \cdot \text{sec}^{-1}$, leaf diffuse resistance rose as an exponential function in all the species observed. In some of the studies, photosynthesis and water use were observed to drop when ODR fell below $20 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \cdot \text{sec}^{-1}$. Whereas stomatal response to low soil O_2 levels was highly consistent, the effect of low soil O_2 on plant water potential was not. This suggests that theories pointing to increased root resistance resulting from low soil O_2 as the cause of stomatal closure do not fully explain some of the observed data. This in turn suggests that stomatal response under the described conditions may not be entirely a passive mechanical response.

INTRODUCTION

The detrimental effect of low soil oxygen (O_2) availability on plant growth and development has been studied for many years. Excellent reviews have been compiled by various groups (Grable 1966; Cannell 1977; Armstrong 1978; and Vartapetian et al. 1978). Certain phenomena related to various physiological responses associated with low soil O_2 levels, however, have only recently been investigated. Because low soil O_2 levels under field conditions occur mainly in the presence of excessive amounts of soil water, it is not surprising that to date little attention has been paid to indicators of plant water status in response to low soil O_2 . One might assume that these physiological indices respond as they do whenever water stress is relieved.

Plant responses to low soil O_2 per se, separate from the high amounts of water present at flooding, however, have in some cases been shown to result in responses the reverse of water stress relief. This is particularly true for observations

of stomatal response (as measured by diffusion porometry) to low soil O_2 levels. This paper reviews reports of plant response to low soil O_2 from several greenhouse studies that point to stomatal closure as O_2 stress increases. Available evidence suggests that increased diffusive resistances and stomatal closure may not be simple passive responses to low plant water potentials resulting from high root resistance under oxygen stress. Stomatal closure at low soil O_2 levels may result from some more active mechanism apart from the soil-plant-atmosphere physical continuum.

SOIL OXYGEN STUDIES

Physiological responses of plants to low soil O_2 levels frequently come from studies of flooding phenomena. Childers and White (1942), for example found that the photosynthesis of apple trees (*Malus sylvestris*) was reduced when roots were submerged in water. Techniques have since been developed to vary soil aeration separately from soil water.

Stolzy et al. (1961) provided indirect evidence that stomatal aperture was affected by soil O_2 status independently of soil water status. In that study, tomato (*Lycopersicon esculentum*) plants were subjected to a range of soil O_2 partial pressures. Plants were grown in soil, and root systems were enclosed in air-tight containers. All plants were maintained at optimum soil water levels, and a range of soil O_2 levels was imposed by passing various partial pressures of O_2 through the sealed root containers. In two series of experiments, plant tops were exposed to airborne oxidants for short periods. The supply of O_2 to the roots (the soil O_2 diffusion rates, or ODR) influenced the severity of oxidant damage to tops. Soils with ODRs of 16 to $24 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$ were not damaged by peroxyacetyl nitrate (PAN) or ozone. Plants growing in soils with O_2 diffusion rates of 34 to $90 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$ were moderately to severely damaged. In addition, plant water use was directly related to ODR (Fig. 1). As the soil-aeration pretreatment was only 40 h, water use differences cannot be attributed to differences in plant growth factors, but, instead, indicate a fairly rapid physiological response. If we assume that stomatal aperture was reduced by low soil O_2 availability, we can explain the reduction in both oxidant damage and water use.

In a later experiment, Stolzy et al. (1964) observed tomato response to soil aeration and ambient ozone. Soil O_2 was again manipulated

by passing nitrogen gas mixtures over the soil-grown roots. A second aspect of the study compared this "artificial" reduction in soil O_2 with flooding. Soil ODR was measured in all treatments. Low soil ODR maintained for 8.5 h decreased plant CO_2 fixation by 50%. Three hours of low soil ODR only slightly affected photosynthesis. The 3-h anaerobic treatment, however, followed by normal aeration for 24 h, reduced aerial ozone damage up to 50%. Anaerobic soil pretreatment also lessened the reduction in photosynthesis subsequently observed during and after the aerial ozone treatment. Again, plant response suggested a reduction in stomatal aperture related to low soil O_2 levels.

The linkage of ozone damage to stomatal aperture was used some years later by Turner et al. (1972) in selecting tobacco (*Nicotiana glauca*) cultivars for resistance to ozone damage. Plants with greater stomatal aperture generally are associated with greater oxidant damage (Engle and Gableman 1966; Rich and Turner 1968; Rich et al. 1970; Dugger and Ting 1970). Therefore, it seems likely that the observed responses in Stolzy's work were due to stomatal closure in response to low ODR.

Sojka et al. (1975) measured increased leaf diffusive resistance (R_s) in wheat (*Triticum aestivum*) grown under soil- O_2 stress. In their study, wheat was grown in equilibrium with 0, 4, and 21% O_2 mixtures passed over the soil surface at 9, 15, and 21°C. A range of soil ODRs was thus created. Diffusive resistance was low (3.1 to 4.9 sec cm^{-1}) for soil ODRs between 134 and $31.7 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$. When ODR dropped to $12.6 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$, however, diffusive resistance increased to 21.7 sec/cm (see Fig. 2). Temperature affected R_s very little. The stomatal responses observed were from well-watered, soil-grown plants (maintained between 0.1 and 0.3 bar matric potential). No apparent relationship of the stomatal closure to xylem pressure potentials was apparent. Interestingly, the inflection point of the R_s versus ODR curve occurs near the $20 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$ ODR value, which has been established as a threshold for physiological response to inadequate soil O_2 (Stolzy and Letey 1962).

Subsequent studies at the University of California at Riverside substantiated stomatal closure due to low ODR in sunflower (*Helianthus* sp.), cotton (*Gossypium hirsutum* and *G. barbadense*), and jojoba (*Simmondsia chinensis*). Reyes (1975) conducted a series of experiments,

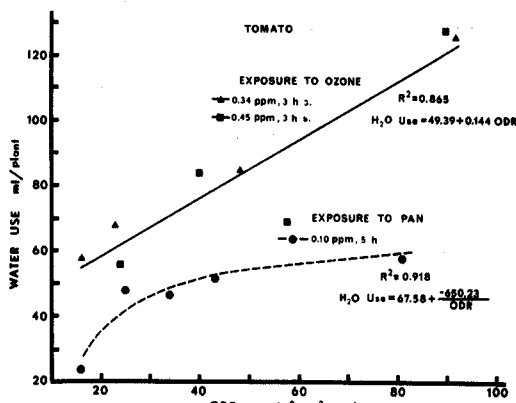


FIG. 1. Water use by tomato plants as a function of soil oxygen diffusion rate (ODR). The top line combines the responses of two 3-h exposure levels of ozone. The bottom line gives the response of plants exposed to ambient peroxyacetyl nitrate (PAN). Adapted from Stolzy et al. (1961).

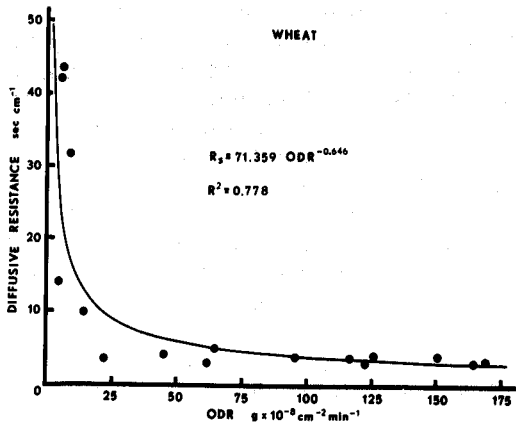


FIG. 2. Diffusive resistance of wheat flag leaves as affected by soil oxygen diffusion rate (ODR). Adapted from Sojka et al. (1975).

using an approach similar to that of the earlier work of Sojka et al. (1975). In Reyes's experiments, plants were grown with roots equilibrated with 0, 4, 12, and 21% O₂ mixtures. Sunflowers were grown at soil temperatures of 9, 15, 21, 27, and 33°C. Because jojoba is a desert plant, it was grown at soil temperatures of 21, 27, and 33°C, only. Leaf diffusive resistance of both sunflower and jojoba increased markedly in response to low soil O₂ availability, particularly in the very low O₂ range (see Fig. 3). The aeration effect on diffusive resistance was highly temperature-dependent for both species. Again, all plants were uniformly maintained at favorable soil matric potentials. A comparison of nighttime *R_s* values and midday values for jojoba (Fig. 4) showed greater differences in *R_s* between treatments at night in the three more favorable O₂ regimes. In this diurnal comparison, the lowest O₂ treatment was deleted, and no separation of *R_s* was observed for daytime observations. This is not unexpected in view of the curvilinear relationship between *R_s* and ODR. The sharp increase in *R_s* would not be expected except at the lowest O₂ treatment, which was not monitored. One other factor that may be considered is that O₂ is produced by photosynthesis in the presence of light. The O₂ produced may diffuse through the plant during the day and partially obscure the *R_s* response to the lowered soil O₂ levels. The separation of *R_s* curves at night, at substantially higher *R_s* values than daytime observations, also indicates that the mechanism bringing about aeration-induced stomatal closure is not a simple, passive physical phenome-

non. This suggests that increased root resistance alone, as has been proposed in the literature (Jackson 1956 and Kramer 1969), is not the sole cause of water stress symptoms in flooded plants, as high root resistance would cause higher daytime *R_s*.

For joboba, *R_s* also increases with increased soil temperatures. Letey et al. (1962a) observed that flooding damage generally is greater during warm weather than during cool weather. This would be expected with the occurrence of stomatal closure because transpirational cooling would be prevented. The temperature × aeration interaction, as Luxmoore et al. (1971), using aeration theory, later explained, is due to a greater demand for O₂ at higher temperatures. They proposed that "induced O₂ shortages" occurred when soil temperature was increased. The induced O₂ shortages result from greater O₂ depletion at higher temperatures due to the

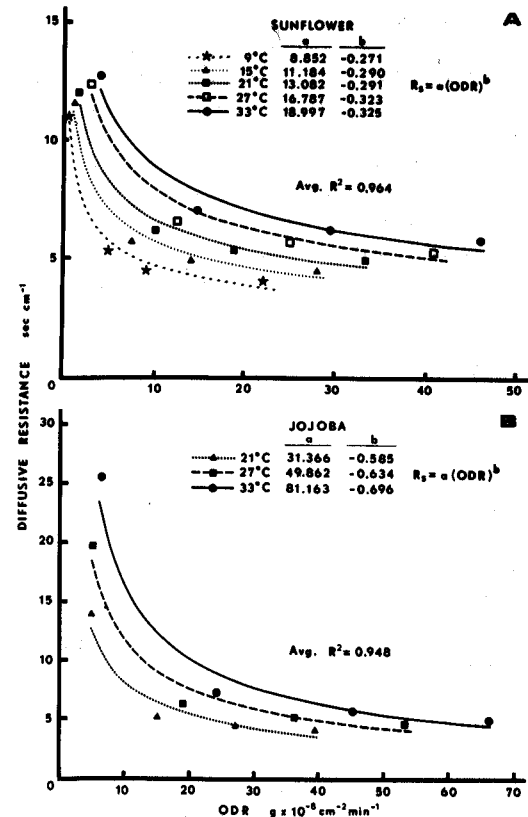


FIG. 3. Leaf diffusive resistance (*R_s*) as a function of soil oxygen diffusion rate (ODR) at various soil temperatures for sunflower (A) and for jojoba (B). Calculated from data presented by Reyes (1975).

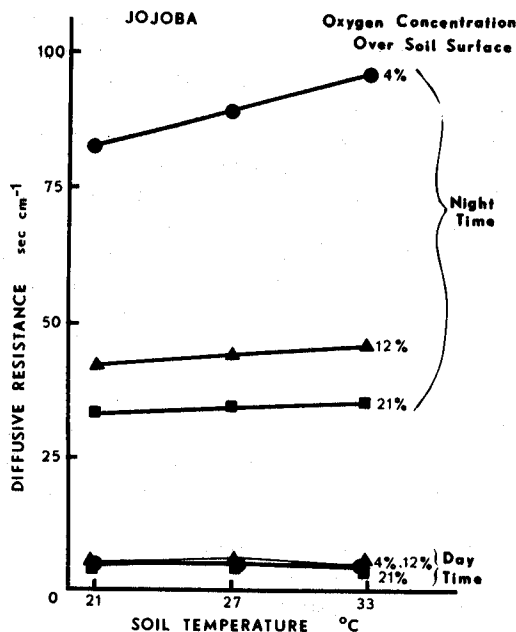


FIG. 4. Leaf diffusive resistance (R_s) of jojoba grown at three soil O_2 levels as a function of soil temperature, as observed at midday and at night. Adapted from Reyes (1975).

elevated respiration rate of both the plant roots themselves and competing microorganisms. Depending on the root respiration rate of a given species, the induced O_2 shortage may result in O_2 depletion extending some distance away from the root (Letey and Stolzy 1967). Because the platinum microelectrode technique of measuring ODR has no way of compensating for these types of plant responses, i.e., increased respiration rates at elevated temperatures, ODR must be calibrated for individual species and conditions to provide greatest reliability.

Reyes observed a decrease in both xylem pressure potential (Ψ_x) and osmotic potential (Ψ_π) corresponding to decreasing soil ODR and increasing soil temperature for tomato, sunflower, and jojoba (unfortunately, Reyes reported no measurements of R_s for tomato). This response, unlike the night response, leads one to suspect a passive physical mechanism affecting stomatal closure, particularly as plant water potential components were especially severely depressed in the treatments of lowest O_2 availability.

In a similar series of well-watered greenhouse experiments, Owen (1977) grew cotton at a soil temperature of 28°C over a range of soil O_2 levels. Soil O_2 treatments were 0, 4, 10, and 21%

O_2 in the equilibrating gas, resulting in ODRs of 3.0, 16.5, 21.5, and $35.5 \times 10^{-8} \text{ g cm}^{-2} \text{ min}^{-1}$, respectively. These ODRs are the average ODRs measured at the 18 and 53-cm depths. In one diurnal study, the R_s 's of the 0 and 21% treatments were compared for four cotton varieties, Stoneville 213, Acala 1517-70, T-4852, and Pima S-4, 45 d after emergence. In this study, diffusive resistance was determined for both sides of the leaf. Diffusive resistance was higher for poorly aerated treatments for both sides of the leaf in all four varieties. The parallel resistances for the two treatments calculated from Owen's diurnal data are averaged across the four varieties in Fig. 5.

In Owen's diurnal data, unlike in Reyes's data, the nighttime R_s of the cotton varieties was higher for the well-aerated treatment. The first pair of night observations are actually nearly the same, whereas the final pair of values are quite dissimilar. We can assume that cotton is more susceptible to water stress than jojoba (a xerophyte) and that, consequently, cotton stomata close more readily in response to water stress. For these reasons, as the plants transpired through the diurnal cycle, poorly aerated plants used less water due to aeration-induced stomatal closure. By the second night, the well-aerated cotton, being more desiccated, showed greater closure (higher R_s) than the poorly aerated cotton. In jojoba, which is less sensitive to drought, the soil matric potential was never low enough to show a drought-induced stomatal response, and the aeration effect alone was observed.

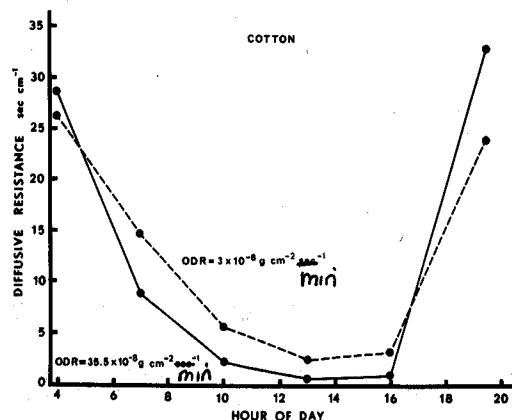


FIG. 5. Average diurnal response of four cotton varieties, showing diffusive resistance (R_s) produced by two levels of soil O_2 . Adapted from Owen (1977).

On days 53 and 93, diffusive resistance, xylem pressure potential, and osmotic potential were determined at midday across all four O_2 treatments and all four varieties. Diffusive resistance increased nearly linearly across varieties as ODR dropped from 35.5 to $3 \times 10^{-8} \text{ g} \cdot \text{cm}^{-2} \text{ min}^{-1}$. As plants aged, the slope of the response line remained about the same, although overall response shifted to a higher range of R_s (Fig. 6). This shift is difficult to interpret. Climatic conditions, soil moisture, leaf temperature, or some combination of these may have been different on the two observation dates. Alternatively, some permanent alteration in leaf morphology or physiology may be associated with aging. Nonetheless, closure of stomata related to decreased soil O_2 availability still occurred. Earlier, Reyes (1975) had suggested that higher R_s in plants grown at low soil O_2 for prolonged periods

could result from a reduction in either the size or the number of stomata per unit area of leaf. Owen's data (1977) suggest that, although this may occur (a shift of the intercept but not of the slope of the $R_s \times \text{ODR}$ response curve), there is still a direct aeration effect (a pronounced slope). Owen did not, however, state the criteria he used to select leaves on the two dates for measurement of R_s . If the same leaf was observed on each date, the leaf may simply have expanded, thereby lowering stomatal density, or may have developed a thicker cuticle layer. If, however, recently matured leaves were always taken from near the top of the plant on each date (leaves of uniform maturity), some other process was affected by the aging, causing greater stomatal closure over the entire range of soil aeration.

In Owen's observation of xylem pressure potential (Ψ_x) and osmotic potential Ψ_π , there was no correlation between R_s and plant water potential. This suggests that stomatal closure is not a simple passive response to internal plant water status. Similar observations were made earlier by Sojka et al. (1975) for Ψ_x in wheat.

In a final greenhouse experiment, Owen observed a single cotton variety, Pima S-4, for its response to ODR and salinity (Fig. 6). The R_s was measured 63 and 84 d after planting. Three salinity levels, 0, 10, and 20 mmho cm^{-1} were achieved by adding NaCl to the soils. Again, R_s increased markedly in response to low ODR; R_s increased with aging; and R_s was not consistently related to plant water potential.

It is worth noting that all the work reported by Stolzy (1961, 1964), Sojka (1975), Reyes (1975), and Owen (1977) was performed using nearly identical soils—Krilium-treated Yolo silt loams or fine sandy loams (Typic Xerorthents). The experimental objectives diverged widely, however, and the individual studies spanned a number of years. Similar results have also been reported by another group working independently, though plants were not grown in soil. Smucker et al. (1975, 1976) found increased R_s due to low root O_2 availability in navy bean *Phaseolus vulgaris* grown in mist culture.

Although the effects of flooding and aeration on plants have been observed by various research groups for many years, few if any direct observations of stomatal response to low O_2 have been made. Kramer (1969) reviewed a large body of information that suggested that flooded plants developed an increased root resistance (though it was not always stated, only higher radial re-

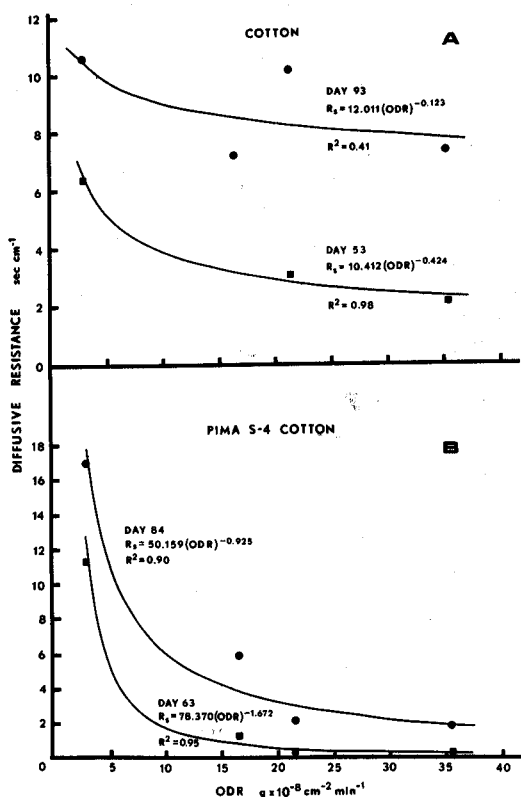


FIG. 6. The effect of aging on the relationship between leaf diffusive resistance (R_s) and soil oxygen diffusion rate (ODR) in cotton. Part A combines the response of four varieties. Part B combines the effects of three salinity levels for the cotton variety, Pima S-4. Calculated from data presented by Owen (1977).

sistance could be expected to produce the effects cited). As an increase in root resistance would reduce the rate of replacement of transpired water, plant water potentials would be expected to drop where there was no change in transpirative demand (Elfvig et al. 1972). Stomata would be expected to begin closing according to this passive and mechanistic rationale, and transpiration would be expected to decrease. In turn, a reduction in transpiration would favor a rise in plant water potential. All these adjustments and environmental feedbacks may result in substantial hysteresis in the diffusive resistance \times water potential loop. Consequently, one might expect a poor relationship between plant water potential and ODR or R_s .

In some of the studies discussed earlier, the effects of flooding on diffusive resistance could be explained by the root-resistance hypothesis (e.g., Reyes's data). In other studies, however, aeration had no detectable effect on plant water potentials, yet diffusive resistance increased as would be expected from stomatal closure (e.g., the data of Owen and Sojka et al.). This would suggest that the increase in diffusive resistance may not always be due solely to passive physical responses to root resistance.

There are at least two mechanisms of nonpassive stomatal closure that may warrant specific investigation in future aeration studies. The first is the involvement, and possible biological production under the conditions described, of such physiologically active chemicals as ethylene, etc. The second is related to alteration of potassium ion flux into guard cells. Plant roots under O_2 stress produce ethanol (Smucker et al. 1979), which is accompanied by plasmolysis of cells in root tips. The combined influence of these factors on stomatal response has not been defined. Ethylene has been found both in soil and in plants (Hunt et al. 1980) grown in poorly aerated soils. Ethylene, a gas, readily diffuses to plant tops from the rhizosphere through the plant. It has been associated also with stomatal closure in plants under drought stress. Similar relationships exist for the respiratory by-product CO_2 .

Potassium ion flux is known to be closely linked with guard cell activity (Macallum 1905; Imamura 1943; Yamashita 1952; Fujino 1959; Fischer 1968, and 1972; Fischer and Hsiao 1968; Humble and Hsiao 1969, 1970; and Humble and Raschke 1971) and to cause the necessary osmotic alterations that induce changes in guard cell turgor. Both Reyes (1975) and Owen (1977)

found decreased levels of K in the tops of the poorly aerated plants. Rains (1968) demonstrated that the ATP expended for stomatal movement in the dark resulted from oxidative rather than photophosphorylation, which may be related to the differences in night and day stomatal response observed by Reyes for jojoba. Virtually all observations of nutrient accumulation in plant tops in response to low soil O_2 have shown significant reduction in K concentration of the plant tops when soil O_2 is limiting (Cline and Erickson 1959; Hammond et al. 1955; Harris and Van Bavel 1957; Hopkins et al. 1950; John et al. 1974; Klotz et al. 1968; Labanauskas et al. 1966a, 1966b, 1968, 1965, 1971, 1972; Lawton 1946; Leggett and Stolzy 1961; Letey et al. 1961a, 1961b, 1965, 1962b; Snow 1936; Sowell and Rouse 1958; Stolzy et al. 1975, 1967; Van Diest 1962; and Wallihan et al. 1961). Cooper et al. (1967) and Peaslee and Moss (1968) showed that elevated K levels increased stomatal aperture and affected stomatal population in alfalfa and corn. Peaslee and Moss speculated that K^+ migration from guard cells of plants under K deficiency caused stomatal closure. It is not clear, however, how long plant roots would have to be deprived of soil O_2 before changes in the shoot nutrient status would occur that could affect stomatal response.

CONCLUSIONS

Because optimizing stomatal response during drought-free periods is important in promoting CO_2 fixation for photosynthesis, factors other than drought that may influence stomatal aperture should be considered. Closure of stomata in response to low light, dry soil, and desiccating ambient conditions is well documented. Information also exists, however, to suggest that substantial stomatal closure (or reduction in pore area if not complete closure) often occurs, even in the absence of significant soil water deficits. The most highly productive agricultural systems are generally either irrigated or in humid or semihumid areas. One may speculate about the possibility that stomatal closure associated with low soil aeration during periods of excess soil water is as significant on a relative basis in such areas as is stomatal closure due to water stress under drought.

The studies we have discussed indicate that the elimination of adequate O_2 from the soil profile can cause stomatal closure. This closure is not fully explained by increased root resist-

ances, as some researchers have suggested. Closed stomata under flooding indicate that guard cells have become flaccid, the microscopic equivalent of wilting in such sensitive plants as tobacco or tomato. Finally, the findings of these various workers indicate that present intuitive assumptions regarding the expected response of plant water status indicators in very wet soils may be suspect. In fact, plant water status indicators in very wet soils become highly unreliable over a wide range of plant species unless corrected to accommodate the substantial interactions brought about by inadequate soil O₂.

It seems evident from the results discussed here and from the amount of supporting research on related phenomena that a definable relationship exists between soil O₂ status and stomatal behavior. The unanswered questions regarding mechanism and nutritional involvement suggest areas for new research.

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